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THE BIOLOGY OF PARADIXA CALIFORNICA

(Diptera: Dixidae)[1]

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This study was made to help fill the need for investigations of the biologies of individual species of the family Dixidae. *Paradixa californica* (Johannsen) was selected because an excellent breeding site was discovered on the University of California campus, where this research was done. Several artificial pools in a courtyard provided all of the ecological factors essential for the support of a large population. Specimens were also collected from numerous creeks and ponds elsewhere in the San Francisco Bay region.

In this paper, after a listing of distribution records for the species, the different stages in the life cycle are discussed, starting with the adult and ending with the pupa. A separate section on methods is not included, because most of the techniques employed are either standard practice in the study of mosquitoes or were mentioned in a recent paper by Nowell (1951).

DISTRIBUTION

In his original description, Johannsen (1923) recorded the type locality of this species as Stanford University, California. Garrett (1924) mentions that two variations of the species occur in British Columbia. About half of the locality records listed below are based upon specimens in the California Academy of Sciences collection (C.A.S.). The remainder of the specimens were collected by the writer, or his associates at the University of California.

CALIFORNIA RECORDS. *Alameda County:* Berkeley, V-23-15 (M. C. Van Duzee) C.A.S.; IV-24-51 (F. Mok); 1950-51 (A. A. Hubert). Castro Valley, IV-10-39 (T. H. G. Aitken) C.A.S. Pleasanton, XI-22-39 (T. H. G. Aitken) C.A.S. *Contra Costa County:* 5 mi. W. Moraga, VI-17-51 (A. A.

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Hubert). *Marin County:* 8 mi S.W. Fairfax, IV-22-51 (C. J. Weinman); VI-23-51 (A. A. Hubert). 2 mi. W. Lagunitas, V-19-51 (C. J. Weinman). Mill Valley, IX-11-45 (E. L. Kessel) C.A.S. Muir Woods Nat. Mon., V-19-15 (M. C. Van Duzee) C.A.S. 2 mi. N. Pt. Reyes Station, V-19-51 (C. J. Weinman). *Mendocino County:* 14 mi. W. Willits, VI-30-51 (W. C. Bentinck). *Monterey County:* Carmel, VII-7-40 (T. H. G. Aitken) C.A.S. Del Monte, X-19-39 (T. H. G. Aitken) C.A.S. *San Mateo County:* San Mateo, IV-42 (E. S. Ross) C.A.S. *San Francisco County:* San Francisco, III-25-26 (M. C. Van Duzee) C.A.S. *Santa Clara County:* Stanford University, 1923? (O. A. Johannsen?); III-29-41 (T. H. G. Aitken) C.A.S. *Sonoma County:* Occidental, IV-22-51 (A. A. Hubert). 3 mi. N. Valley Ford, VII-14-51 (C. J. Weinman).

BRITISH COLUMBIA RECORDS. 1924? (C. B. D. Garrett.)

THE ADULT

General Habits. The adults of this species do not seem to differ in their general habits from those of other kinds of dixids observed. They prefer to rest head upward in places close to the water that are shaded, cool, and moist. On rock surfaces they are found from a few inches to three feet above the water. In the artificial pool, where many observations were made, they were noticed to congregate in the corners. It was also in these corners that most of the egg masses were found. Adults were frequently captured in hollows beneath dirt banks among the roots of plants. In steep seepage areas they will rest on the thick wet moss. The only time when this species was observed to rest on the leaves of shrubs was in the evening. Dixidae seem to undergo a daily migration from the moister and more sheltered niches close to the stream in the middle of the day, to the overhanging or bordering vegetation in the cool of the evening.

Very little time during the daylight hours is spent in actual flight. The flights, when they do occur, are low and of short duration. When *P. californica* adults are disturbed, they fly a short distance along the bank and land again. At times they will fly out from the bank and return almost to the exact spot which they left. An individual will often hover at several places along the margin of a stream or pool before choosing a resting place.

The Question of Feeding.—It has been generally accepted that adults of the family Dixidae do not feed. This deduction has been based principally upon the poorly developed mouthparts, which are evidently not adapted for biting. However, Malloch (1917) reported that he found adults on flowers, apparently feeding on

nectar. Montschadsky (1936), in contrasting the Dixidae with the Culicidae, claimed that the former are plant feeders.

Adults of *Paradixa californica*, kept in an insect cage, were observed to land on some apple slices and go through the motions of feeding. Each apparently feeding individual crouched with its body tilted at a slight angle to the apple and brought its mouthparts in contact with the moist surface. It seemed to feed on one spot for a while, and then spend some time exploring and probing with its proboscis. However, all motions of the latter sort were barely perceptible to the unaided eye. On another occasion a female was seen while evidently attempting to feed on a dried out slice of apple. A bowl of water was kept in the cage at all times.

During the summer of 1951 a number of females were seen in the typical feeding or drinking attitude on the bank of one of the artificial pools previously mentioned. Most of these were on damp areas of the concrete bank, but one was crouched where the bank was dry. The flies would maintain this position for several minutes at a time, and no motion could be detected. These observations were made during daylight.

The most plausible explanation for this behavior is that the dixids are seeking moisture. However, the proximity of water in all cases, and the apparent restriction of this habit to females, indicate that they might actually be feeding. In any case, feeding is not essential, because adults will mate, oviposit, and live as many as fifteen days without taking any nourishment.

Longevity.—Previous estimates of the length of dixid adult life fell far short of the averages recorded for *Paradixa californica.* For example, Nowell (1951) stated that adult dixids usually live two to three days. The over-all average for 16 individuals timed by the writer was nine and one-half days. All specimens lived at least four days, and the maximum time recorded was 15 days. On the average the females lived slightly longer than the males. In order to obtain the above figures, pupae were reared in individual vials, and the dates that the adult emerged and died were noted. In each vial was a wad of cotton moistened with water, but no food material. Most of the vials were kept in the laboratory at an average temperature of 70.8 degrees Fahrenheit. A cooler environment lengthened the life expectancy.

Mating Habits.—There are two distinct patterns in the mating procedure of *Paradixa californica.* In one of them no swarming of

the males takes place, and mating occurs during daylight. The other involves swarming flights and takes place in the evening. The swarming of dixid males has been mentioned many times in the literature, but the other pattern has not been previously reported.

Although mating of the first type can occur during any kind of weather, it is most often seen on cool overcast days. The first case of this kind was observed on the bank of the artificial pool in April, 1951. Others were seen throughout the remainder of spring and summer. On most such occasions the adults engage in short individual flights along the bank and do a considerable amount of hovering. The males are slightly more active in this respect than the females.

In mating a male flies over to a resting female and half flies, half climbs onto her back. Mounting results in the male facing in the same direction as the female. The male next climbs backward over the larger female and gropes for the tip of the abdomen with his terminalia. While continuing in his attempts to bring the genitalia together, he climbs over the side of the female and underneath, until he is suspended below her body in an inverted position. Union of the copulatory organs occurs in this position. Usually the female raises her hind legs, enabling the male to pass under more easily. Actual copulation lasts from a few seconds to several minutes.

The writer was not fortunate enough to witness any swarming flights until a still evening in June, when several separate swarms were seen. The adults had congregated on the undersides of the leaves of a large bush on the bank of the pool. Several males would begin flying opposite the end of a branch until seven or eight individuals were swarming in a rather tight formation. The flight of each consisted of a constant rising and falling with a change in elevation of about three inches. Very little horizontal distance was covered in these maneuvers. No actual copulations were seen, although several couples paired off for a few seconds. From time to time adults of either sex would drop out of the formation and land on the lower side of a leaf.

Nowell (1951) records that female dixids fly down through the center of a swarm, become paired with males, and the fused couples settle on leaves or rocks below. He states that copulation is com-

pleted in about a minute, and then the males fly back up into the swarm.

Oviposition.—When ready to oviposit, the female *Paradixa californica* locates a rock, or other suitable substratum with a moist surface. Sheltered corners or areas hidden by plants are preferred to unprotected spaces. The gravid female comes to rest at a point about an inch above the surface of the water, and her abdomen begins a series of pulsations, each one of which carries the tip closer to the substratum. Soon after the tip has made contact, the first white eggs appear and are attached to the bank by the gelatinous substance in which they are enclosed. Laying of the entire egg mass takes about half an hour.

Little difficulty is encountered in inducing females to oviposit in captivity. A bowl with a small amount of water and an emergent rock for the attachment of egg masses are all that is necessary. Oviposition can occur within five days after mating.

THE EGG

Development.—Each egg consists of an elliptical white central

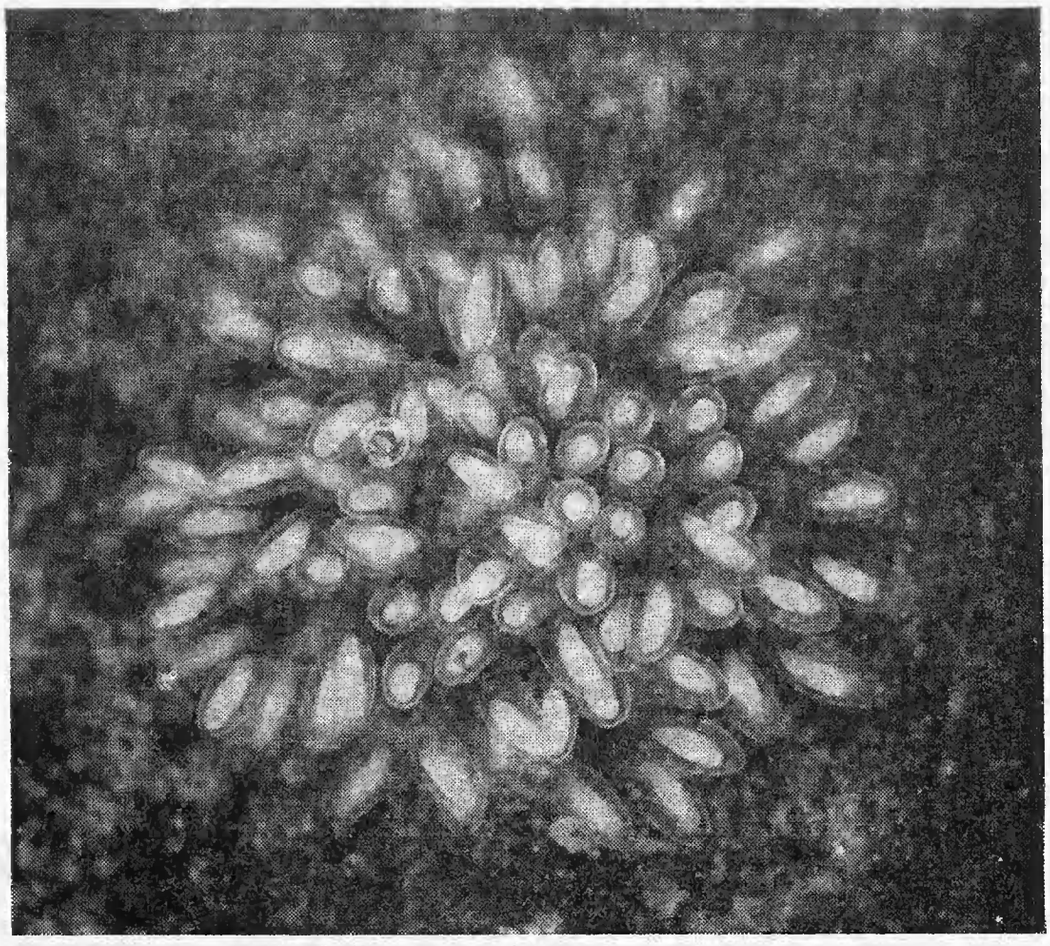

Fig. 1. Egg mass of *Paradixa californica*

portion surrounded by a more transparent capsule. These eggs are imbedded in a perfectly clear gelatinous mass, which is attached to a rock or floating branch at, or a short distance above the water-line. As the partially submerged mass matures the gelatinous matrix tends to disintegrate, and some eggs may even become free and sink to the bottom. By the fourth or fifth day after oviposition, larvae can distinctly be seen within the eggs. The head can be distinguished from the rest of the body, which is bent back on itself. The extremities may be directed toward either end of the egg. The eyes, prothoracic setae, and caudal bristles are visible.

A few hours before the eggs are ready to hatch, the larvae may be seen to move and reverse position within their egg capsules, which gradually weaken and become quite flaccid. The activity of the larvae increases until they are turning and twisting with great vigor. Emergence is achieved by thrusting repeatedly against the weakening apex of the egg with either end of the body or the middle loop, until a rupture is finally forced. The larva may come forth in any position, depending on when the retaining membrane gives way.

The maximum number of eggs counted in any mass was 100 and the minimum was 42. The average for six egg masses was 75 eggs. The egg stage average five days in length at room temperature. No significant difference was noted at a temperature ten degrees cooler.

Ability to Withstand Desiccation.—A chip of wood having several attached egg masses in various stages of development was removed from the water and placed in an empty bowl. For two days the wood was kept only slightly damp, and for three more days it and its egg masses were allowed to desiccate completely. At the end of this period the egg masses had become reduced to some stained areas on the dry wood. The chip was placed in a bowl of water, and at once the water was literally covered with hundreds of wriggling first instar larvae. Apparently development continued to an advanced stage despite the five days that the eggs were out of water.

Further evidence that at least a certain amount of desiccation might not be abnormal in the development of the eggs of this species was derived from an examination of masses along the bank of the pool where most of these studies were made. The masses

varied in height from half an inch to fully two inches above the water surface. Most of these were on damp areas, but others were apparently isolated by recession of the water. Fluctuations in the level of the pool take place periodically, and many of the eggs laid undergo this drying before they are inundated by a subsequent rise in the water level. Admittedly this is an artificial situation, but this adaptation must also aid in the survival of the species under more natural conditions.

THE LARVA

General Characteristics.—The larvae of *Paradixa californica* may be found along the margins of slowly flowing creeks, and in small ponds and pools, both natural and artificial. They assume the usual dixid position on a moist surface with the middle of the body looped away from the water, and both head and posterior end in the positive meniscus. Rocks and floating branches are the favorite resting places, but occasionally larvae will crawl up on emergent vegetation. Shade is always preferred to sunlight.

Although the larvae require an aquatic environment, they do not hesitate to crawl up out of the water on the moist surface of a rock or plant stem. Comstock (1924) best characterized the typical dixid method of terrestrial locomotion when he reported that larvae progress by alternate thrusts of the two ends of the body, the bent portion travelling foremost. The larvae of *californica* have paired prolegs on the first and second abdominal segments, and a series of ambulacral combs on the fifth through seventh abdominal segments, which alternately provide an anchorage enabling the opposite side of the body to advance. At all times the larvae are covered with a thin film of water. This not only provides protection against desiccation, but it supplies them with a smooth wet surface on which to slide.

The larvae of this species swim awkwardly and rather slowly. The anterior half of the body swings forcefully to one side, the bend occurring at about the fourth abdominal segment, and the posterior half also moves to the same side. Then the process is reversed, the middle loop exchanging sides with both ends of the body.

The various instars feed exclusively on material floating in the surface film of water. The head is tilted back until it is almost ventral side up, and a current created by the labral and maxillary mouth brushes conveys all small particles to the mouth. Everything

is taken into the mouth, but the larva lowers its head to a horizontal position and egests larger pieces of inorganic material.

Reactions to Stimuli.—When disturbed, a larva on a wet rock surface will crawl away from the source of irritation with one or two quick thrusts of the body. If teased with a brush from the direction of the water, it will move up the rock until the stimulus is discontinued. Similarly, if prodded from above, it can be induced to reverse the direction of its body loop in one motion and swim out from the rock.

A sudden bump against the container, or a prod with the brush, will sometimes cause a swimming or floating larva to thrust itself away from the surface film and sink down a short distance. If the water is shallow, it will lie motionless on the bottom with its body bent. It will swim back up to the surface after a few seconds if the stimulus is not repeated. The spiracular lobes and lateral lobes of the caudal end are folded inward holding a bubble of air over the spiracles during these dives. This escape mechanism enables the larvae to elude predators at the water surface.

Parasites and Predators.—Since Nowell (1951) discussed the enemies of dixid larvae at some length, this account will be limited to the writer's experience regarding *Paradixa californica.* A hydrophilid larva of the genus *Tropisternus,* which was collected with some dixids of this species, had captured one of the latter when taken. Another *Tropisternus* kept in a bowl of water was observed to capture and eat a larva.

Some larvae being reared by the writer became infected about the anal area with what appeared to be a fungus. Dr. E. A. Steinhaus, insect pathologist at the University of California, was kind enough to examine the infected specimens. His findings showed the presence of large numbers of rod-shaped bacteria gathered about the caudal end of the larvae. Cultures of the gelatinous mass of bacteria yielded abundant growth of a gram-negative short rod that did not ferment lactose. A gram-negative yellow pigmented rod (probably a *Flavobacterium*) was also present, but this was believed to be an adventitious species. No fungi were apparent either on the larval specimens or the culture plates.

Rate of Development.—The length of the different instars was determined by rearing the larvae from the egg stage. It was necessary to collect third instar larvae and rear the fourth instars individually after they molted, due to the high mortality and slow

development. Most of the rearing was done either outside or in the laboratory in finger bowls containing pond water. The water was changed frequently to prevent the development of bacteria and to introduce a fresh supply of food. The over-all average length of the first instar was six and one-half days, of the second instar 10 days, of the third instar 13 days, and of the fourth instar 33 days. The average length of 63 days thus computed for the larval stage is undoubtedly much longer than would be the case in the natural habitat. If the minimum times for each of the four instars are totalled a length of 43 days is obtained.

THE PUPA

The larvae of *Paradixa californica* always climb up out of the water to pupate. Most pupae are found attached by their side to the substratum a short distance above the surface of the water. They remain in this position, with the abdomen tightly curled about the cephalothorax, until the emergence of the adult. If they are loosened accidentally by the current, they will float in the water dorsal side up with the respiratory trumpets breaking the surface. Emergence of the adult will take place whether the pupa is attached to the bank or is in the water. However, the newly-emerged adult is very fragile and is easily drowned.

A pupa that has recently shed its last larval skin still retains a limited motility. The abdomen is not so firmly appressed to the cephalothorax and can be used in crawling. An early pupa on a wet rock surface can be induced to crawl away from a point of irritation with surprising rapidity. It does so by straightening and curling the abdomen. In this early stage the pupa can also right itself in the water. The inability to move, which develops later, is due to a hardening of the pupal skin.

Of all the stages in the life cycle, the length of the pupal stage is the mot constant. In the laboratory it almost invariably lasted three days. Four days was the longest time recorded.

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ANOTHER SPECIES OF RHAMPHOMYIA PREDACEOUS ON MOSQUITOES (Diptera: Empididae)[1] A species of *Rhamphomyia* was reported by Frohne (1952. Mosquito News, 12 [4]:263) as being a water-level predator of emerging mosquitoes in Alaska. The flies were said to be of small size, and the wings were described as "smoky." Both sexes were assumed to be predaceous. In July, 1952, some medium-sized empidids with similar predatory habits were collected by the writer in the Bitterroot Mountains of southwestern Montana. These flies, which have clear wings and are evidently a different species from those observed by Frohne, were tentatively identified by Mr. G. E. Shewell of the Canadian Department of Agriculture, Ottawa, as *Rhamphomyia (Megacyttarus) argenteus* Bigot. They were observed flying back and forth at a height of six to twelve inches above sunlit alpine pools, frequently darting to the surface of the water to capture pupae and newly emerged adult mosquitoes. Small bits of twig and other floating particles were struck in flight and immediately released. All specimens in a small series collected at each of two sites were males. In one place the mosquitoes being preyed upon were *Aedes nearcticus* Dyar and *Aedes hexodontus* Dyar; in another they were a species of *Culiseta*. The elevations of these localities were 7,500 feet and 8,300 feet respectively.—ALEXANDER A. HUBERT, Rocky Mountain Laboratory, Hamilton, Montana.

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[1] From the Federal Security Agency, Public Health Service, National Institutes of Health, National Microbiological Institute.